

Xanthomonas campestris pv. poaeのPoa属植物に対する病原性の多様性

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Pathogenic Diversity of *Xanthomonas campestris* pv. *poae* within the Genus *Poa**

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Abstract

The diversity of pathogenicity of *Xanthomonas campestris* pv. *poae*, the causal agent of bacterial wilt in the genus *Poa*, was studied. Strains of *X. c.* pv. *poae* were distinguishable into three groups, according to differences in their pathogenicity against *Poa* species. Group 1, represented by strain JT-P192, caused mild wilt and a pale yellow appearance in leaves of annual bluegrass and supina bluegrass. Group 2, represented by strain JT-P482, was pathogenic to annual bluegrass, rough bluegrass and supina bluegrass, but caused only wilt symptoms. Group 3 included the type strain of *X. c.* pv. *poae*, which caused only a wilt in annual bluegrass, rough bluegrass, supina bluegrass and big bluegrass. Compatible and incompatible relationships were evaluated from the symptoms on infected plants and from bacterial multiplication in the lowest part of the culm after leaf clipping-inoculation.

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Key words : pathogenicity, multiplication, *Poa* genus, *Xanthomonas campestris* pv. *poae*.

INTRODUCTION

Xanthomonas campestris pv. *poae*, the causal agent of bacterial wilt of *Poa* species, is distributed throughout Europe^{5,6,18}, the U. S.^{12,16} and Japan¹⁰⁻¹². This pathogen is localized in the vascular systems of host plants. *X. c.* pv. *poae* from Switzerland was first reported by Egli and Schmidt⁶; rough bluegrass (*Poa trivialis* L.) was very susceptible, whereas annual bluegrass (*P. annua* L.) was only moderately susceptible. Recently, bacterial wilt of annual bluegrass has also been found in the U.S.¹⁶ and in Japan^{10,11}. Identified as *X. c.* pv. *poae*, these newly found bacteria are strongly aggressive on annual bluegrass but not on rough bluegrass¹² and are distinguishable into two groups according to the symptoms or disease severity in annual bluegrass¹². One group causes mild wilt and/or pale yellow discoloration limited to leaf blades, and the other causes severe systemic wilt.

Because *X. c.* pv. *poae* causes a severe wilt on annual bluegrass, it has been investigated as a biological control agent against annual bluegrass in the U. S.^{8,19} and in Japan^{1,2,13,14}. Annual bluegrass is a problematic weed due to the lack of selective herbicides for its control in intensively managed turfs⁴. About 500 species of the *Poa* genus are distributed throughout the world¹⁵, including beneficial turf grasses, such as Kentucky bluegrass (*P. pratensis* L.). However, the pathogenicity of newly found strains of *X. c.* pv. *poae* on *Poa* species has not been

investigated.

To elucidate the pathogenic diversity of *X. c.* pv. *poae* among the *Poa* genus, we studied symptoms on 23 cultivars from nine species of *Poa* inoculated with 10 strains of *X. c.* pv. *poae*, and measured bacterial multiplication in the plants after leaf clipping-inoculation⁹.

MATERIALS AND METHODS

Bacteria and plants The bacterial strains tested in this study are listed in Table 1. The American strains, MB218, MB245 and MB291, were provided by the Mycogen Corporation, and the type strain of *X. c.* pv. *poae* ATCC33804 was provided by the American Type Culture Collection (ATCC).

Plants for inoculation tests included two cultivars of annual bluegrass (originating in Japan and in the UK.), six cultivars of rough bluegrass (cv. Omega, cv. Sabre, cv. Colt, cv. Laser, cv. Dasas and one originating in the UK.), nine cultivars of Kentucky bluegrass (*P. pratensis* L. cv. Ken Blue, cv. Merit, cv. Coventry, cv. Adelphi, cv. Baron, cv. Raml, cv. Banff, cv. Nassau and one originating in the UK.), supina bluegrass (*P. supina* Schrad. cv. Supina), big bluegrass (*P. ampla* Merr. cv. Sherman), Canada bluegrass (*P. compressa* L. cv. Ruebens), sandberg bluegrass (*P. secunda* Presl cv. VNS), bulbous bluegrass (*P. bulbosa* L., cultivar unknown) and alpine bluegrass (*P. alpina* L., cultivar unknown). Annual bluegrass originating in Japan was provided by Utsunomiya

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Table 1. Strains of *Xanthomonas campestris* pv. *poae* used in this study

Strains	Original host plant	Locality	Other features (Reference)
JT-P192	Annual bluegrass	Aomori Pref. in Japan	Group 1 (12)
JT-P195	do	do	do (this study)
JT-P196	do	Aichi Pref. in Japan	do (12)
JT-P481	do	Tochigi Pref. in Japan	Group 2 (12)
JT-P482	do	Kanagawa Pref. in Japan	do (12)
JT-P484	do	Chiba Pref. in Japan	do (12)
MB218 ^{a)}	do	U.S.A	do (12)
MB245	do	do	do (12)
MB291	do	do	Group 1 (this study)
ATCC33804 ^{b)} (Xg724)	Rough bluegrass	Switzerland	Group 3 ; Type strain of <i>X. c.</i> pv. <i>poae</i> ; (6)

a) Strain MB218, MB245 and MB291 were provided by Mycogen Corp.

b) ATCC : American Type Culture Collection.

University. The other species of *Poa* were provided by the Mycogen Corporation, except for plants originating in the UK., which were purchased from Herbiseed (Wokingham, England, UK.).

Inoculation Seeds were sown in plastic pots of organic soil and grown in a greenhouse at 25°C/20°C (day/night) for 4 weeks.

Bacteria were cultured in YNB¹²⁾ liquid medium at 28°C for 2 days on a rotary shaker until the early stationary growth phase. Bacterial cells were then collected by centrifugation and resuspended in equal volumes of sterile distilled water. The bacterial suspensions were diluted to a final concentration of 10⁸ cfu/ml, by comparison with an absorption curve at 575 nm, to prepare the inocula. Plants, 4 weeks after sowing, were inoculated by means of leaf clipping-inoculation⁹⁾. The inoculated plants were all grown under the same greenhouse conditions, both to observe disease severity and to investigate bacterial multiplication in the plants.

Measurement of disease severity Disease severity in inoculated plants was assessed according to the following five criteria : A : severe attack, all plants died ; B : heavy attack, plants wilted with only 30% remaining green ; C : moderate attack, plants wilted but later regenerated, growing pale yellow new leaves ; D : slight attack, only clip-inoculated leaves wilted ; E : no attack, plants remained entirely healthy. The disease index was calculated according to the following formula :

Disease index (%)

$$= \frac{A \times 4 + B \times 3 + C \times 2 + D \times 1 + E \times 0}{(A + B + C + D + E) \times 4} \times 100$$

Measurement of bacterial multiplication in plants

Two methods were used to assess bacterial multiplication in plants after leaf clipping-inoculation. To count the number of viable bacteria in the vascular systems of inoculated plants, 5 mm lengths of tissue samples from the inoculated leaf tips and the lowest parts of the culm were collected from inoculated plants which had been surface-sterilized by wiping with cotton dipped in 70% ethanol. Collected tissue samples were cut into five pieces in 200 µl of sterile distilled water and shaken gently for ca. 30 min to isolate the bacteria in the vascular systems. The suspensions were diluted serially and spread on to YNA¹²⁾ plates containing 200 µg/ml of cycloheximide to count the number of viable cells. The other method was simply microscopically checking for bacterial exudation from vascular tissue samples excised from inoculated plants set in a drop of water.

RESULTS

Aggressiveness of each strain against *Poa* species

Four weeks after inoculation, annual bluegrass, rough bluegrass, supina bluegrass and big bluegrass showed symptoms from some strains of *X. c.* pv. *poae*. However, Kentucky bluegrass, Canada bluegrass, sandberg bluegrass, bulbous bluegrass and alpine bluegrass showed no typical symptoms from any of the tested strains (Table 2). When the disease index was under 30%, no typical symptoms were observed. Strain JT-P192 caused heavy symptoms (disease index of about 50%) on annual bluegrass and caused moderate symptoms (disease index of about 30%) on supina bluegrass and on two cultivars of rough bluegrass (cv. Omega and the one originating in the UK.). Strain JT-P482 caused moderate to heavy symptoms on rough bluegrass and caused plant death in annual bluegrass and supina bluegrass. Strain ATCC33804, the type strain of *X. c.* pv. *poae*, caused heavy symptoms on rough bluegrass, moderate symptoms on annual bluegrass and supina bluegrass, and caused plant death in big bluegrass.

Multiplication in plants

The multiplication of three strains of *X. c.* pv. *poae* in four species of *Poa* which showed symptoms from some strains of *X. c.* pv. *poae* was examined. Annual bluegrass originating in the UK., rough bluegrass originating in the UK., supina bluegrass and big bluegrass were used as the test plants. All tested strains of *X. c.* pv. *poae* (JT-P192, JT-P482 and ATCC33804) multiplied in a similar manner in the inoculated leaf tips of all tested plants (Fig. 1). In the inoculated leaf tips, bacteria multiplied to about 10⁷ cfu/5 mm length of the leaf tissue until 5 days after inoculation, and then the bacterial population declined. This decline of bacterial populations in the inoculated leaf tips was related to the wilt of

Table 2. Disease severity on *Poa* species inoculated with different strains of *X. c. pv. poae*

Plants inoculated (origin or cultivar)	Disease index ^{a)} (%)		
	JT-P192	JT-P482	ATCC33804
Annual bluegrass			
<i>Poa annua</i>			
(originating in the UK.)	58.3±4.8	100.0±0.0	36.7±4.1
(originating in Japan)	58.3±4.7	100.0±0.0	41.7±4.7
Rough bluegrass			
<i>P. trivialis</i>			
(originating in the UK.)	30.0±2.7	46.7±6.8	51.7±5.2
(cv. Omega)	33.3±3.1	46.7±4.8	58.3±4.7
(cv. Sabre)	25.0±0.0	38.3±4.1	46.7±4.8
(cv. Colt)	26.7±1.7	35.0±3.3	48.3±4.5
(cv. Laser)	28.3±2.3	38.3±4.8	48.3±4.5
(cv. Dasas)	28.3±2.3	38.3±5.4	70.0±4.4
Kentucky bluegrass			
<i>P. pratensis</i>			
(originating in the UK.)	26.7±1.7	15.0±3.3	16.7±3.1
(cv. Ken Blue)	18.3±3.0	11.7±3.3	16.7±3.1
(cv. Merit)	25.0±0.0	21.7±3.3	20.0±2.7
(cv. Coventry)	15.0±3.3	13.3±3.3	11.7±3.3
(cv. Adelphi)	15.0±3.3	16.7±4.0	13.3±3.3
(cv. Baron)	25.0±0.0	16.7±3.1	18.3±3.0
(cv. Raml)	18.3±3.0	20.0±3.6	15.0±3.3
(cv. Banff)	20.0±2.7	18.3±3.0	15.0±3.3
(cv. Nassau)	13.3±3.3	16.7±4.0	15.0±3.3
Supina bluegrass			
<i>P. supina</i>			
(cv. Supina)	33.3±3.1	100.0±0.0	33.3±3.1
Big bluegrass			
<i>P. ampla</i>			
(cv. Sherman)	10.4±3.7	17.5±3.8	100.0±0.0
Canada bluegrass			
<i>P. compressa</i>			
(cv. Ruebens)	21.7±2.3	16.7±3.1	10.0±3.3
Sandberg bluegrass			
<i>P. secunda</i>			
(cv. VNS)	6.7±3.0	20.0±5.6	15.0±3.3
Bulbous bluegrass			
<i>P. bulbosa</i>			
(cultivar unknown)	25.0±0.0	23.0±2.1	16.7±4.2
Alpine bluegrass			
<i>P. alpina</i>			
(cultivar unknown)	6.7±3.0	6.7±3.0	13.3±3.3

a) Each value is the mean (disease index±standard error) of 15 replications of inoculated plants.

leaves. Test bacteria were not able to maintain their populations in the inoculated leaf tips of their host plants, because the inoculated leaf tips dried out 4 weeks after inoculation when inoculated leaves had wilted severely. Typical symptoms were not observed in rough bluegrass which had been inoculated with strain JT-P192 or in big bluegrass which had been inoculated with either strain JT-P192 or JT-P482. In these cases, bacterial populations in the inoculated leaf tips did not decline rapidly.

Multiplication in the lowest part of the culm differed in different strain/plant combinations (Fig. 2). Strain JT-P192 was able to multiply in the lowest part of the

culm of annual bluegrass and supina bluegrass. Strain JT-P482 was able to multiply in the lowest part of the culm of annual bluegrass, rough bluegrass and supina bluegrass. Strain ATCC33804 was able to multiply in the lowest part of the culm of annual bluegrass, rough bluegrass, supina bluegrass and big bluegrass. In annual bluegrass/pathogen combinations in 5 mm of tissue segments, strain JT-P482 multiplied to about 1.0×10^9 cfu, strain JT-P192 multiplied to about 1.0×10^7 cfu, and strain ATCC33804 multiplied to about 1.0×10^4 cfu. The multiplication rate of strains in the lowest part of the culm in annual bluegrass was correlated with the plants' disease severity. This relationship between the multipli-

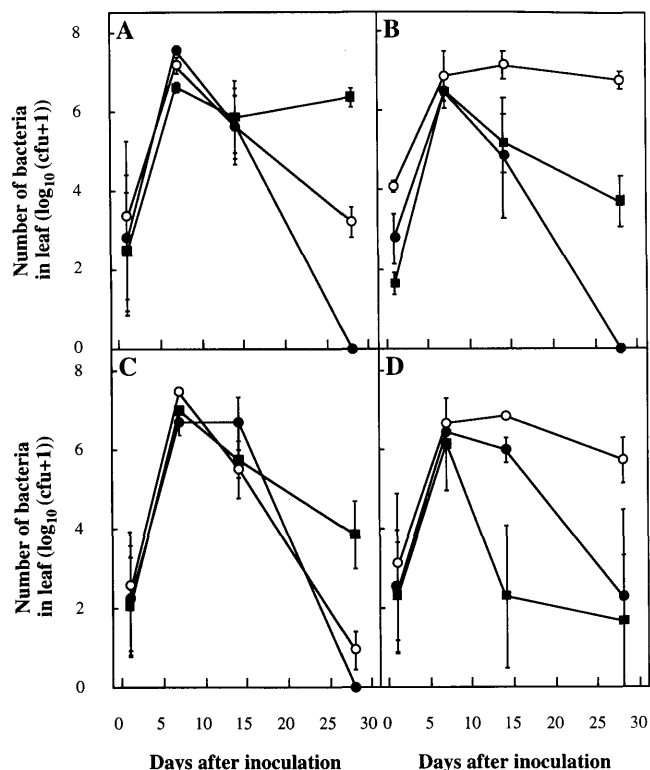


Fig. 1. Multiplication of strains of *X. c. pv. poae* in 5 mm sections of leaf tissue from the inoculated leaf tip of *Poa* species. Annual bluegrass (*P. annua*) (A), rough bluegrass (*P. trivialis*) (B), supina bluegrass (*P. supina*) (C) and big bluegrass (*P. ampla*) (D) were inoculated with 1.0×10^8 cfu/ml of bacterial suspension of JT-P192 (○), JT-P482 (●) and ATCC33804 (■) by leaf clipping-inoculation. Inoculated plants were grown in the greenhouse at 25°C/20°C (day/night temperature). Bars indicate standard error ($n=3$).

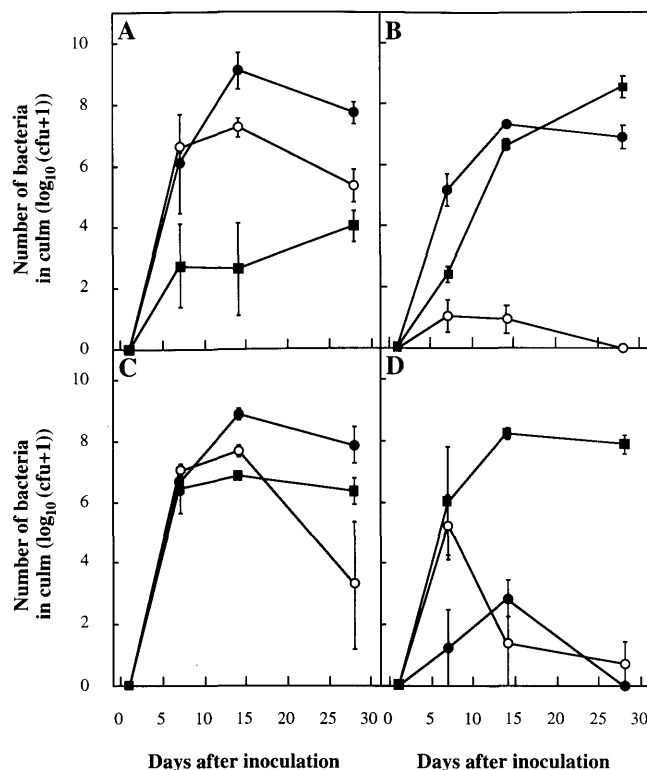


Fig. 2. Multiplication of strains of *X. c. pv. poae* in 5 mm sections of tissue from the lowest part of the culm of *Poa* species. Annual bluegrass (*P. annua*) (A), rough bluegrass (*P. trivialis*) (B), supina bluegrass (*P. supina*) (C) and big bluegrass (*P. ampla*) (D) were inoculated with 1.0×10^8 cfu/ml of bacterial suspension of JT-P192 (○), JT-P482 (●) and ATCC33804 (■) by leaf clipping-inoculation. Inoculated plants were grown in the greenhouse at 25°C/20°C (day/night temperature). Bars indicate standard error ($n=3$).

Table 3. The symptoms produced on *Poa* species inoculated with 10 strains of *X. c. pv. poae*

Plant inoculated	Symptoms ^{a)}									
	JT-P192	JT-P195	JT-P196	JT-P481	JT-P482	JT-P484	MB 218	MB 245	MB 291	ATCC 33804
Annual bluegrass	W/C	W/C	W/C	W	W	W	W	W	W/C	W
Rough bluegrass	—	—	—	W	W	W	W	W	—	W
Supina bluegrass	W/C	W/C	W/C	W	W	W	W	W	W/C	W
Big bluegrass	—	—	—	—	—	—	—	—	—	W

a) w/c, wilt and chlorosis; w, wilt only; —, no symptom.

cation rate in the lowest part of the culm and aggressiveness was observed in all strain/plant combinations.

Microscopic observations 4 weeks after inoculation showed no bacteria in the lowest part of the culm of the other *Poa* species, Kentucky bluegrass, Canada bluegrass, sandberg bluegrass, bulbous bluegrass and alpine bluegrass.

Symptoms of host plants

Symptoms of four species of *Poa* inoculated with 10 strains of *X. c. pv. poae* were observed after inoculation

(Table 3), using the same plants as those used in the examination of bacterial multiplication. Four strains, JT-P192, JT-P195, JT-P196 and MB291, caused wilt and chlorosis on their host plants, annual bluegrass and supina bluegrass. Newly elongated leaves after infection were a discolored, pale yellow. Five strains, JT-P481, JT-P482, JT-P484, MB218 and MB245, caused wilt on annual bluegrass, rough bluegrass and supina bluegrass. Type strain of *X. c. pv. poae*, strain ATCC33804, caused wilt on annual bluegrass, rough bluegrass, supina blue-

Table 4. Features of three groups of *X. c. pv. poae*

	Representative strain	Symptoms on host plants	Pathogenicity to rough bluegrass	Pathogenicity to big bluegrass
Group 1	JT-P192	W/C ^{a)}	— ^{b)}	—
Group 2	JT-P482	W	+	—
Group 3	ATCC33804	W	+	+

a) w/c, wilt and chlorosis ; w, wilt only.

b) +, showing pathogenicity ; —, no pathogenicity.

grass and big bluegrass.

DISCUSSION

In this study, a disease index of 30% was used as a borderline between the presence and absence of typical symptoms. From this basis, strain JT-P192 caused symptoms in annual bluegrass, supina bluegrass and two cultivars of rough bluegrass (cv. Omega and the one originating in the UK.). However, JT-P192 was unable to spread to the lowest part of the culm of rough bluegrass after leaf clipping-inoculation. Because of this and the fact that ethylacetate extracts of culture filtrate of JT-P192 show phytotoxic activity (data not shown), strain JT-P192 may produce phytotoxic compounds in inoculated leaves of rough bluegrass, which cause the symptom-like effects on rough bluegrass.

In many cases, both compatible and incompatible bacteria multiply within the inoculation zone^{3,7)}. Robinson and Callow, studying the multiplication and spread of the xylem-invading xanthomonads *X. c. pv. poae* and *X. oryzae* pv. *oryzae* in rough bluegrass¹⁷⁾, reported that both compatible and incompatible bacteria could multiply within inoculation zones at similar rates but that their migration through plants varied. Compatible bacteria were distributed throughout host leaves, whereas the spread of incompatible bacteria was limited to the inoculation zone. Results from the present study showed that all strains were able to multiply in the inoculated leaf tips at the same rate but that multiplication in the lowest part of the culm varied with different plant/strain combinations. In our method, the multiplication in the lowest part of the culm was correlated with bacteria distribution throughout the inoculated leaves, from inoculated tip to the lowest part of the culm. Using this pathogenicity trait of compatibility and the ability to distribute throughout leaves of host plants, strain JT-P192 is compatible with annual bluegrass and supina bluegrass, strain JT-P482 is compatible with annual bluegrass, rough bluegrass and supina bluegrass, and type strain of *X. c. pv. poae* ATCC33804 is compatible with annual bluegrass, rough bluegrass, supina bluegrass and big bluegrass. *X. c. pv. poae* strains, however, are not compatible with the other tested plants, Kentucky bluegrass, Canada bluegrass, sandberg bluegrass, bulbous bluegrass and alpine bluegrass. Multiplication in the lowest part of the culm also corresponds to symptom appearance and its rate to disease severity.

Egli and Schmidt⁶⁾ reported that *X. c. pv. poae* showed pathogenicity to the *Poa* genus, although considerable differences in susceptibility are found at the species level. In our previous report¹²⁾, we reported that the bacteriological properties of test strains, JT-P192, JT-P482 and ATCC33804, were the same and that their host range was limited to the *Poa* genus. We now propose that *X. c. pv. poae* should be divided into three groups with the same pathovar status (Table 4). Group 1 causes pale yellow discoloration of new elongated leaf blades and wilt to annual bluegrass and supina bluegrass. Group 2 causes wilt to annual bluegrass, rough bluegrass and supina bluegrass. Group 3, which includes the type strain of *X. c. pv. poae*, causes wilt to annual bluegrass, rough bluegrass, supina bluegrass and big bluegrass. Representative strains of group 1 and group 2 are strain JT-P192 and strain JT-P482, respectively.

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和 文 摘 要

西野友規・藤森 嶺： *Xanthomonas campestris* pv. *poae* の *Poa* 属植物に対する病原性の多様性

日本およびアメリカで分離されたスズメノカタビラに萎ちょう症状を引き起こす *Xanthomonas campestris* pv. *poae* のうち任意に選抜した9菌株と *X. c.* pv. *poae* の標準菌株である ATCC33804 株を用いて、9種23系統の *Poa* 属植物に対する病原性を、(1) 病気を引き起こすか、(2) 植物内で増殖・移行できるか、(3) 宿主植物の病徴はどのようなものか、という3項目について調査した。剪葉接種法により接種試験を行ったところ、すべての菌株はすべての供試植物の接種部位において増殖したが、地際部での細菌の増殖にはそれぞれの組み合わせにおいて差がみられ、病徴の有無と地際部での細菌の増殖には相関関係が存在していた。その結果、*X. c.* pv. *poae* は *Poa* 属植物に対する病原性の違いから3グループに区別されることが明らかとなった。すなわち *X. c.* pv. *poae* は、スズメノカタビラと *supina* bluegrass に対して病原性を示し、その病徴が萎ちょう症状と葉の黄化症状である JT-P192 株に代表されるグループ1、スズメノカタビラ、*rough* bluegrass、*supina* bluegrass に対して萎ちょう症状のみを引き起こす JT-P482 株に代表されるグループ2、そしてスズメノカタビラ、*rough* bluegrass、*supina* bluegrass、*big* bluegrass に対して萎ちょう症状のみを引き起こす標準菌株である ATCC33804 に代表されるグループ3に区別される。